

REPRODUCTION, HABITAT UTILIZATION, AND MOVEMENTS OF HOGFISH (*LACHNOLAIMUS MAXIMUS*) IN THE FLORIDA KEYS, U.S.A.: COMPARISONS FROM FISHED VERSUS UNFISHED HABITATS

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ABSTRACT

Few studies conducted within marine reserves have compared the behavior of exploited reef fishes within protected and fished areas to test the hypotheses that reproductive output, habitat utilization, and fish movements differ between management zones. We conducted 134 hrs of snorkel and scuba surveys in the Florida Keys National Marine Sanctuary in the Western Sambos Ecological Reserve (closed to fishing) and the adjacent Middle Sambos site where fishing is permitted. At these sites we gathered detailed information on microhabitat utilization of hogfish, *Lachnolaimus maximus* (Walbaum, 1792), their movements, encounter rates, and reproductive behavior. Most of the data were collected with focal animal observations by snorkelers and the behavioral data geographically logged with a hand-held GPS. Multivariate analyses of microhabitats present on home ranges and utilized by hogfish indicate no overall differences between the protected vs fished site, yet at both sites male movements were more widespread than those of females. Despite an extensive survey effort within the fished site, virtually no reproductive activity was observed there, compared with 55 spawning events recorded from six different harems within the reserve. Though not significantly different, underlying trends that we observed for hogfish encounters and movements between study sites are consistent with the idea that key social processes differ between sites. These data suggest a breakdown of social structure at the fished site and highlight the role that marine reserves may play in the maintenance of reproductive output by exploited site-attached fishes with complex social and mating systems.

No-take marine reserves are primarily established with two main fisheries management goals: recruitment subsidies, or the net export of larvae from the reserve to fished areas, and spillover, or the net movement of juveniles or adults to fished areas (Gell and Roberts, 2003; Halpern, 2003; Bartholomew et al., 2008). Recruitment subsidies should arise from the enhanced reproductive output and greater spawning stock biomass of large-bodied protected stocks. Indeed, a growing number of studies indicate that the size, biomass, density, and diversity of organisms tend to be higher inside than outside reserves (Williamson et al., 2004; Ault et al., 2006; Molloy et al., 2008), and evidence continues to accumulate that demonstrates increases in biomass of reproductively active fish with reserve protection (e.g., Plan Development Team, 1990; DeMartini, 1993; Sale et al., 2005).

Despite data indicating generally positive effects on fish populations within marine reserves, it has been suggested that confounding factors, lack of suitable control sites, and critical knowledge gaps necessitate caution when utilizing such evaluations to shape management policy (Willis et al., 2003; Sale et al., 2005; Tetreault and Ambrose, 2007). In addition, there remains a dearth of definitive evidence in support of recruitment subsidies from reserves to adjacent fisheries and very few

studies have tried to measure the impact of reserves on reproductive output (but see Branch and Odendaal, 2003; Evans et al., 2008). Others caution that higher densities of large individuals in reserves could reduce spawning frequency or numbers of eggs per batch through competition for food or space (Roberts and Polunin, 1991). Additionally, numerous species use specific sites for spawning which makes them particularly vulnerable to fishing, and protection of these sites could enhance spawning success (Beets and Friedlander, 1999; Nemeth et al., 2007). Unfortunately, few no-take reserves have explicitly incorporated spawning sites into their boundaries (but see Burton et al., 2005) and the fact remains that there are many fishery species for which more basic ecological information is required before inferences about the efficacy of reserves in their management become possible (Petersen and Warner, 2002; Sale et al., 2005).

Spillover can theoretically occur in a number of ways, including random movements of fish, diffusion from high density (reserve) to low density (outside reserve), directed daily migrations, ontogenetic habitat shifts, or in response to space limitations and aggressive interactions associated with greater densities and average size of targeted organisms in reserves (Russ, 2002; Abesamis and Russ, 2005; Tupper, 2007). Crucial information gaps concerning fish movements persist, however, that inhibit understanding of the existence and extent of spillover from reserves (Kramer and Chapman, 1999; Sale et al., 2005). Although studies are accumulating that attempt to measure the magnitude of fish movements or how they are influenced by environmental variables (Helfman et al., 1982; Chapman and Kramer, 2000; Eristhee and Oxenford, 2001; Meyer and Holland, 2005), the home range sizes, activity patterns, and habitat preferences of many species of exploited fishes remain unknown (Tupper and Rudd, 2002; Lowe et al., 2003).

Reserves are believed to function well for protecting small, site-attached species such as reef fishes which are generally more sedentary (or home ranging) than other comparably sized vertebrates (Choat, 1991; Sale, 1991). Some reef fishes, however, display extensive daily movements (e.g., 5-ha home ranges, Chateau and Wantiez, 2007) or undertake lengthy (18 to > 185 km) seasonal or annual migrations to spawning sites (McGovern et al., 2005; Nemeth et al., 2007), and there is concern that most economically important species may be too mobile to benefit from reserve protection (Sale et al., 2005). On the other hand, even for fish capable of moving long distances, tagging studies have revealed that some members of the population appear relatively sedentary and capable of benefiting from the protection of a reserve while others undertake significant movements that make them available to fishers outside the reserve (Gell and Roberts, 2003). Differing movements within a population could be related to fidelity to specific sites or higher quality habitat associated with reserves (Koenig et al., 2000; Roberts, 2000; Rodwell et al., 2003) and restricted movements within reserves could alter any spillover effect desired. Clearly, further study of the behavior and mobility of exploited species is needed as these parameters can be critical to the successful functioning of reserves designed for fisheries management (Kerwath et al., 2007; Afonso et al., 2008).

As an initial step in better understanding the effects of marine reserves on recruitment subsidies and spillover, we designed a study that aimed to investigate the following two predictions: (1) reproductive output in a no-take reserve should be greater than in an adjacent fished area as a result of reserve protection; (2) habitat utilization and fish movements should differ between management zones (reserve and fished ar-

eas), possibly related to higher quality habitat associated with the reserve. We tested these predictions in the Florida Keys National Marine Sanctuary (FKNMS) with the economically important, sex-changing hogfish, *Lachnolaimus maximus* (Walbaum, 1792). Intensive, high-resolution behavioral observations of focal hogfish revealed dramatic differences in reproductive output between management zones that may result from a breakdown of social structure at the fished site.

METHODS

Our study was conducted from March 2004 through March 2006 in the Sambos region of the FKNMS, located approximately between 24°28'–24°30'N and 81°39'–81°43'W. Divers with the United States National Marine Fisheries Service (NMFS) have conducted annual monitoring of reef fishes and associated benthic habitats since 1979 in the Florida Keys (Bohnsack et al., 1999) and these data were used to select our study sites. We chose sites based on high densities of hogfish and similarity of benthic habitats as recorded by the NMFS survey and where distinct management regimes were in place (no-take reserve vs fishing permitted). The reserve site, the Western Sambos Ecological Reserve, was designated a no-take zone in July 1997, although snorkeling and scuba diving are permitted. The reserve extends from the shoreline to the 18.5 m depth contour, encompasses approximately 3000 ha, and contains the greatest habitat diversity in the lower Florida Keys (U.S. Department of Commerce, 1996). The study site open to fishing was located in the Middle Sambos area, approximately 2.6 km from the reserve. Both study sites share a variety of habitats including shallow spur and groove, drowned spur and groove, back reef, and reef rubble areas (Florida Fish and Wildlife Conservation Commission, 2000). Consequently, the Middle Sambos site has been used as an open reference site by a variety of investigators comparing processes occurring in reserves with those from open areas, including studies of queen conch (*Strombus gigas* Linnaeus, 1758) and Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804), and studies of ecological processes and ecosystem function with corals and fishes (Keller and Donahue, 2006). At both sites, we conducted our observations where water depths ranged from 1 to 8 m and where underwater visibility ranged from approximately 8 to 12 m. Further details of the study areas can be found in Jaap (1979), U.S. Department of Commerce (1996), and Cox and Hunt (2005).

Lachnolaimus maximus is the largest western Atlantic wrasse, estimated to reach a maximum size of approximately 16 kg, and is a highly prized food fish (Davis, 1976; McBride and Richardson, 2007). A prominent black spot on the body behind the pectoral fins differentiates males from females (see Colin, 1982; McBride and Johnson, 2007, for further details of coloration). It is a protogynous hermaphrodite (sex change from female to male) and is typically found along the sandy margins of reefs where single males appear to maintain territories and harems of between 10–15 females, with which they spawn on a daily basis during the afternoon (Colin, 1982). Colin (1982) suggested that these harem territories may also be feeding areas and noted that they were defended from other males. Tupper and Rudd (2002) found that catch per unit effort (CPUE) of hogfish was inversely related to distance from the center of a no-take reserve, suggesting that spillover of this species could enhance yields on fished reefs.

The desirability and economic importance of hogfish, relative site attachment, and a daily spawning habit during a protracted (or continuous) spawning season (November through June in Florida, peaks from December through April; Davis, 1976; McBride and Johnson, 2007) make *L. maximus* an ideal study organism for an investigation of reproductive output and utilization of space within the context of a no-take marine reserve. Furthermore, because protogyny occurs in many species that are heavily harvested and important components of tropical fisheries (e.g., Serranidae, the groupers; Scaridae, the parrotfishes; Reeson, 1983; Thompson and Munro, 1983; Russ and Alcala, 1989; Jennings et al., 1995), a study of the sex-changing hogfish should not only provide general insights for how site-attached or territorial

reef fishes respond to reserve protection, but may also illustrate some responses that may be unique features of the protogynous life history.

We gathered data pertaining to hogfish reproduction, movements, microhabitat utilization, and habitat availability. All behavioral observations were conducted on snorkel. Reproductive observations were conducted during January through March to coincide with peak spawning (Davis, 1976; McBride and Johnson, 2007). We conducted daily spawning observations of six focal males with hand-held GPS units attached to surface floats (Garmin Map 76, accurate to 3–5 m, see Nanami and Yamada (2008) for a similar approach). We synchronized a watch with the GPS units and recorded the time of all significant behavioral events (see below). By maintaining position directly above focal hogfish, the GPS units provided tracks that could be geo-referenced with GIS software to produce positional information of focal animals, locations of spawns, conspecifics encountered, and spawning territory boundaries. We confirmed reproductive activity via visual observations of spawning fishes. Data gathered included the frequency, location, and timing of spawning, harem size (number of females that spawned with a particular male), and sizes of males and females (total length [TL], estimated by comparing the size of a focal animal against an object on the reef, which was later measured; Muñoz and Motta, 2000). The daily spawning period for many territorial wrasses is associated with conspicuous patrolling behavior during which a male navigates his entire territory and passes close by and interacts with each female he encounters (Colin and Bell, 1991). As the end of the daily spawning period draws near males noticeably decrease the swimming speed of patrols (Colin, 1982) and resume non-reproductive behavior including feeding activity and visits to cleaning stations (R. Muñoz, unpubl. data). Therefore, we considered that the entire series of spawning events for a particular harem had been fully characterized for that day if the following three conditions were met: (1) we initiated observations before a focal male had begun his afternoon patrolling behavior, (2) our observations continued uninterrupted until patrolling speed decreased and non-reproductive behaviors were observed, (3) observations continued for at least 20 min following the last observed spawn. Determining the entire series of spawning events allowed us to estimate daily reproductive output for individual social groups, calculated as the total number of eggs spawned and estimated by the number and sizes of females observed to spawn per harem together with known body size-fecundity relationships (Davis, 1976; McBride et al., 2008).

We characterized the movements of hogfish ($N = 54$) outside the afternoon spawning period with GPS units and hour-long focal observations (as above) of male and female hogfish, during which we recorded all conspecifics encountered. The movements (area traversed per observation period, in m^2) of hogfish were taken directly from the GPS units. These units calculate the area of a particular track based on the external edge of the total number of track points (locations) that are automatically recorded during an observation period. The units determine the area of an irregular shaped home range by adding together its smaller subunits. Collectively, these data allowed an estimate of number of conspecifics encountered per unit area (hectare) and were used to estimate the relative abundance of hogfish in the reserve vs the fished site.

We determined the microhabitat utilization patterns of male and female hogfish ($N = 36$) with 20 min focal observations and instantaneous sampling made outside the afternoon spawning period (Martin and Bateson, 1993; Muñoz and Motta, 2000). Briefly, we recorded the composition of the substratum immediately beneath the focal animal every 15 s.

We quantified microhabitats present on hogfish home ranges with randomly placed, 25 m linear point-intercept transects (e.g., Miller and Gerstner, 2002), and recorded substrata lying under points at 25 cm intervals along the transects ($N = 107$). This yielded 100 points per transect, each of which was randomly placed eight times per home range. Substratum categories included algal turf (multispecific, oftentimes filamentous assemblage approximately 1–10 mm in height), sandy turf (algal turf laden with sediment, characteristic of lower wave exposure), turf/macroalgae (algal turf mixed with sparse macroalgae, which are fleshy and typically > 10 mm in height), sand, gorgonian, sandy rubble, rubble, live coral, and macroal-

gae. We also quantified rugosity for each transect by conforming a 6 m long chain (approx 1.5 cm links) to the sea floor and comparing its length with a measuring tape used to determine the flat distance covered by the chain. The ratio of chain length to tape length gives the rugosity index, with perfectly flat surfaces characterized by indices of one, and increasingly rugose surfaces characterized by indices greater than one (Risk, 1972).

Our general approach was to locate a focal hogfish, turn on the GPS unit to initiate tracking, and following a five to ten minute acclimation period, begin hour-long observation periods of hogfish movements. Of that hour-long period, the last 20 min were used for the simultaneous collection of both movement and microhabitat utilization data. We concluded these observations following an estimate of fish size. We later used the geo-referenced track log of individual hogfish movements to locate the approximate central area of movements, then used the GPS units to navigate back to this core area and used this core area as the starting point for benthic transects to characterize habitat availability. Observations that took place during the afternoon spawning period followed a similar approach except our focus was on the collection of reproductive data and these observations continued until the spawning period was judged complete for the evening (described above). Our plan was to devote an equal amount of time to work in the reserve and fished site to acquire approximately equal sample sizes from both locations. We alternated days of work in both study sites but subsequently devoted considerably more effort to surveys for reproductive behavior in the fished site when our initial surveys at that site failed to locate spawning hogfish.

We used PRIMER (Ver 6, Warwick, 1993; Warwick and Clarke, 2001) and one way analysis of similarities (ANOSIM) tests to conduct multivariate analyses of microhabitats present on home ranges, to compare microhabitat utilization patterns of hogfish from the reserve vs the fished area, and to compare microhabitat utilization patterns with the distribution of microhabitats in the environment. This latter comparison revealed a significant difference, so a similarity percentages (SIMPER) analysis was used to determine the contribution of particular microhabitats responsible for the observed dissimilarity. As an independent estimate of microhabitat preferences by hogfish, we calculated Jacobs' (1974) improved estimate of Ivlev's electivity index: $D = (r - p) / \{(r + p) - 2rp\}$ where r = the proportion of a given microhabitat utilized by *L. maximus* and p = the proportion of that microhabitat available in the environment. D has a range from -1.0 to +1.0, with negative values indicating avoidance, zero indicating random selection from the environment, and positive values indicating active selection or preference. Prior to parametric tests, we verified for normality and homoscedasticity with the Kolmogorov-Smirnov and Levene median tests, respectively. Rugosity indices were reciprocal $\log_{10}(x+0.5)$ transformed to correct for non-normality and compared between sites with a t -test. We used the Mann-Whitney Rank Sum test to compare observation period lengths as these data were not normally distributed. We used separate two-way ANOVAs to test for the effects of sex and study site on both hogfish size and their movements. Movement data were \log_{10} transformed to correct for non-normality and heteroscedasticity. Significant differences were isolated with the Student-Newman-Keuls test. We used linear regression to examine the relationship between the number of daily matings and male size (cm TL). We could not complete meaningful statistical tests of encounter rates between the sexes and between study sites. These comparisons suffered from low statistical power attributable to the difficulty of gathering behavioral data in the field, and partly attributable to the natural biology of *L. maximus* that is characterized by a harem mating system with a population sex ratio skewed towards females. We estimated the relative abundance of hogfish in the reserve vs the fished site by comparing conspecific encounters per hectare of focal females (a larger sample size than for males) between study sites.

RESULTS

REPRODUCTIVE ACTIVITY AND REPRODUCTIVE OUTPUT.—Although Colin (1982) reported that hogfish spawning began in mid afternoon in Puerto Rico, we initially wanted to determine if the onset of reproductive activity took place at alternate times at our study sites in the Florida Keys, so we paid careful attention to the behavior of focal fish throughout the day (0800–1800) during preliminary surveys for reproductive behavior. We never observed spawns before 1500 and therefore settled on a start time for observations of reproductive behavior at approximately 1400. Our observations of hogfish movements, encounter rates, and microhabitat utilization, as well as transects for microhabitat availability were conducted outside the afternoon spawning period (approximately 0800–1400).

Spawning took place in the afternoon from approximately 1500 to 1800. At these times males could be found actively patrolling distinct areas of the sea floor (or harem spawning territories), characterized by extended bouts of conspicuous swimming along predictable routes. These patrols were interrupted only by aggressive chases of males encountered or bouts of courtship that were initiated repeatedly with any female encountered, eventually culminating in successive pair spawning events with individual females (see Colin, 1982, for further details). Patrolling resumed immediately following each social interaction and feeding by males was rarely observed during these spawning periods. A resumption of feeding activity, decrease in swimming speed, and abandonment of patrol route, together, indicated the end of the daily spawning period. Table 1 summarizes the study effort and reproductive behavior recorded from the reserve and fished area. Despite approximately three times greater effort spent searching for reproductive behavior and 3.8 times greater area surveyed in the fished site, no spawning was observed there. We did observe one incidence of courtship on our last day of research at the fished site but poor visibility and fading daylight precluded further observations. In contrast, we recorded 55 spawns from six different harems in the reserve, and fully characterized reproductive activity from five of these harems (i.e., we recorded spawns from one harem after only 8 min of observation so this harem was not included in analyses). As expected for a species with a harem mating system, males were significantly larger than females in both the reserve and fished sites, although within-sex size differences between the sites were not evident (mean \pm SE total length, males: reserve – 39.9 ± 1.3 cm, fished – 39.3 ± 2.2 cm; females: reserve – 29.4 ± 1.2 cm, fished – 31.4 ± 1.3 cm; two-way ANOVA, sex: $F_{1,45} = 30.95$, $P < 0.0001$; site: $F_{1,45} = 0.20$, $P = 0.66$; sex \times site: $F_{1,45} = 0.62$, $P = 0.44$).

Table 1. Summary of study effort and reproduction observed for *Lachnolaimus maximus* in the Florida Keys. Data were recorded from six different reproductive harems but only five were fully characterized (see Methods). * = a single occurrence of courtship was observed; N/A = not applicable.

Factor		
Study site	Western Sambos	Middle Sambos
Status	Reserve	Fished
Reproductive survey effort	7 hrs	19 hrs
Area surveyed for reproduction	2.5 ha	9.6 ha
Spawns observed	55	0*
Reproductive harems characterized	6 (5)	N/A
Total hours of observation	134 hrs	

Table 2. Summary of daily reproductive data recorded from *Lachnolaimus maximus* in the Western Sambos Ecological Reserve, Florida Keys. N = 5 spawning territories.

Factor	Mean	SE	Range
Active spawning (min)	49	7.84	29–62
Number of spawns	5	1.45	1–8
Courtship effort (No courtship events/30 min)	7.79	2.35	1.40–16.03
Chase effort (No chases/30 min, 65% directed at males)	1.49	0.47	0.33–2.88
Spawning territory area (m ²)	1,378	205.87	821–1,766

The maximum number of spawns per male that we observed was eight (for a 48 cm TL fish), compared to another male (35 cm TL) that only spawned once (Table 2). There was a positive but non-significant trend between male size (cm TL) and the number of daily matings attained (number of matings = $-11.3 + [0.406 \cdot \text{TL}]$; $r^2 = 0.445$; $P = 0.23$). These differences in number of spawns attained were associated with large differences in courtship effort, with the 35 cm male expending more than double the courtship effort of the 48 cm male (16.0 vs 7.8 bouts of courtship per 30 min, respectively). Spawning territories averaged 1300 m² and active spawning lasted nearly an hour.

Harem spawning territories were clustered along the benthos, sometimes contiguously, and were persistent through time (compare Fig. 1A with Fig. 1B). We also illustrate another male (presumably subordinate) that attempted to acquire a territory between the two previously established territories (an interstitial territory) nearly two months later (Fig. 1C), and the effect that this subordinate male had on the established male's territory (Fig. 1D), resulting in a minor adjustment to his territory boundary and some overlap between the two territories.

Observations of neighboring males recorded during the spawning period revealed variation in mating success (Fig. 2). The established male spawned eight times compared to only twice for the subordinate male. Note that courtship of females occurred throughout the territory of the established male and spawns also were not restricted to a specific location on the territory. Aggressive interactions (chases) between both males, in contrast, were all located near their territory border. In fact, concurrent spawning observations with these two males revealed that the subordinate male crossed the territory boundary while the established male was on the opposite side of his territory and spawned with a female in this male's territory. We were unable to determine if the female that spawned with the subordinate male was regularly associated with the established male, but this alleged sneak spawn (a spawn between a neighboring male and a female normally associated with a territorial male that occurs while the territorial male is temporarily absent, Warner and Robertson, 1978) illustrates one reason why aggressive interactions are associated with territorial boundaries. In general though, aggressive behavior between males or between females was rarely observed outside the spawning period and males did not appear to defend their territories throughout the day. In addition, repeated daily spawning observations made on the same individual male *L. maximus* indicate high congruence in the total number of spawns achieved on successive days (R. Muñoz, unpubl. data), but female *L. maximus* were not as individually recognizable as males and the fidelity of females to a strict harem remains to be investigated.

Given data from spawning behavior that we observed together with harem characteristics that we recorded, including sizes of males and females, harem size, frequency of spawning, and previously established female body size-fecundity relationships

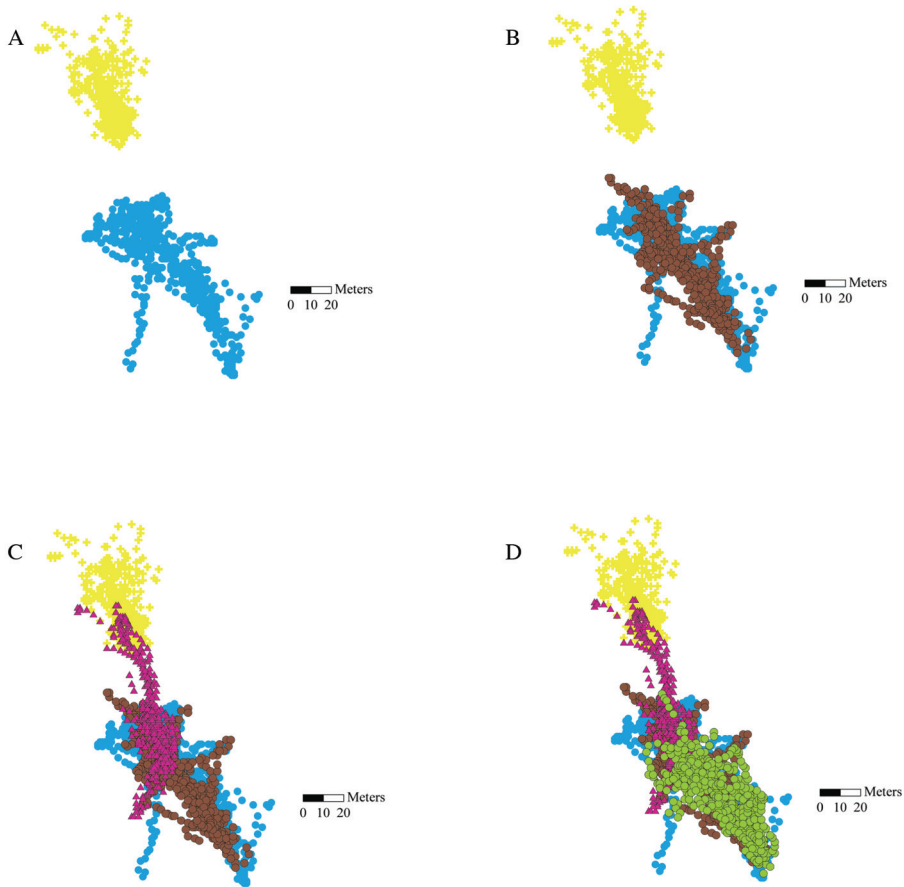


Figure 1. Representative spatial arrangement of three *Lachnolaimus maximus* spawning territory harems from the Western Sambos reserve recorded with hand-held GPS. The exact locations of our observations are not listed due to sensitivity of the data. Different colors either represent different male territories or different observations of the same male made on successive days. (A) Territories of two males tracked continuously during the spawning period of 21 January 2005. (B) Territory of “blue” male (now shown with brown circles) tracked on 24 January 2005. (C) Territories of same two males from (A) and (B), including an additional male (red triangles) tracked on 19 March 2005 utilizing an interstitial territory (Nursall, 1977) and apparently achieving inferior results (see Fig. 2). (D) Shift in movements by “blue” male tracked on 19 March 2005 (green circles) in response to interstitial territory of subordinate male (red triangles). Note the high degree of similarity in movements of the “blue” male recorded between days, between months, and when faced with potential competitors for reproductive space.

(see Methods), daily reproductive output for a representative harem in the ecological reserve containing eight females would be approx. 32,000 eggs.

BENTHIC HABITATS.—We found broad overlap in the microhabitats that characterize the benthos available to hogfish in the reserve and fished area (Fig. 3, one way ANOSIM, $R = 0.041$, $P > 0.05$). For example, macroalgae, sandy turf, and algal turf are the three most common microhabitats at both locations and microhabitats with lower percent cover (e.g., live coral, sandy rubble) are also similar between sites. Mean rugosity indices between study sites were not significantly different (mean \pm SE for reserve [$N = 52$] vs fished site [$N = 54$], respectively: 1.24 ± 0.02 vs 1.23 ± 0.03 ,

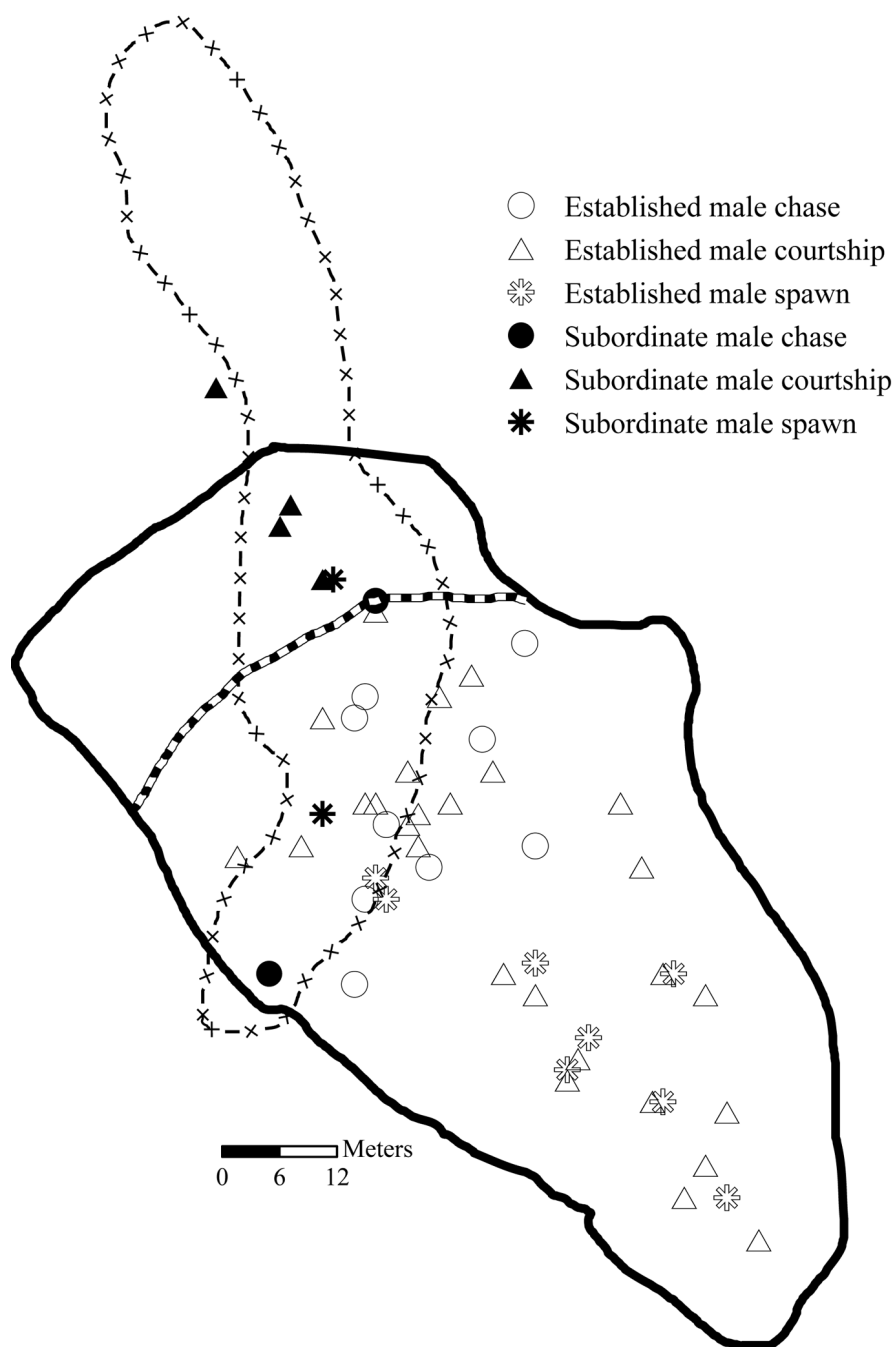


Figure 2. Behaviors recorded during the spawning period from two adjacent *Lachnolaimus maximus* harem spawning territories on 19 March 2005 from the Western Sambos reserve. Aggressive chases, courtship, and spawns were recorded for both males but the frequency of these behaviors varied dramatically between males. Territory borders are illustrated by circumscribing the majority of GPS tracks. Original territory border of established male is indicated with a solid black line. Heavy dashed line indicates the relocation of territory border by established male in response to interstitial territory of subordinate male. X-line indicates territory border of subordinate male.

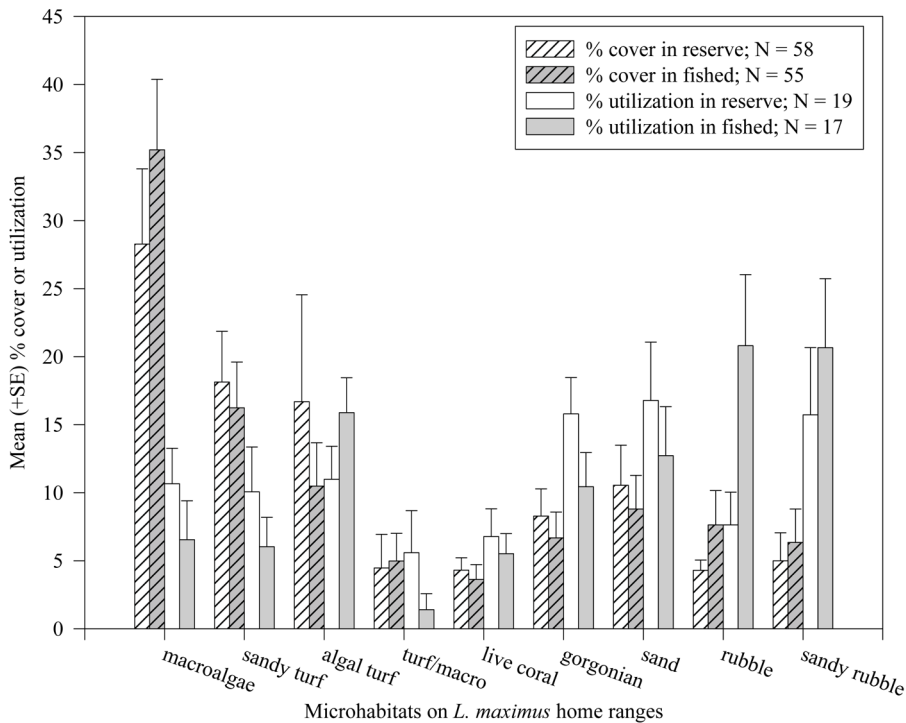


Figure 3. Distribution of benthic microhabitats and microhabitat use behavior by *Lachnolaimus maximus* from Western Sambos reserve and Middle Sambos fished site.

$t_{0.05} = -0.933$, $P = 0.353$). Similarly, we also found considerable overlap in the pattern of microhabitat utilization by hogfish in the reserve and fished site (Fig. 3, one way ANOSIM, $R = 0.045$, $P > 0.05$), such as hogfish at both sites occurring most frequently over sandy rubble, sand, and gorgonian habitats. Subsequently, data from both sites were pooled for comparisons of utilization vs availability on the sea floor. This analysis revealed that hogfish did not utilize microhabitats in relation to their availability in the environment but rather selected sandy rubble, rubble, sand, and gorgonians while primarily avoiding macroalgae and sandy turf habitats, results corroborated by Jacobs' electivity index (Fig. 3, Table 3, one way ANOSIM, $R = 0.324$, $P < 0.001$).

MOVEMENTS, ENCOUNTER RATES, AND RELATIVE ABUNDANCE.—Despite the similarity between sites in benthic habitats and in habitat utilization by hogfish, males in both sites engaged in greater movements than females (Fig. 4, two-way ANOVA, sex: $F_{1,50} = 8.04$, $P = 0.007$; site: $F_{1,50} = 0.28$, $P = 0.60$; sex \times site: $F_{1,50} = 0.08$, $P = 0.77$). Male hogfish at the fished site appear to make extensive movements though high variability obscured significant differences within males between sites.

Observations of focal fish indicate that females are encountered more often than males but social encounters do not differ between study sites (Fig. 5). Although non-significant, the underlying trends suggest that female hogfish may encounter males or females more often at the fished site than in the reserve (Fig. 5A,C) while males may encounter females more often in the reserve than at the fished site (Fig. 5D).

Table 3. Summary of SIMPER and Jacobs' electivity index results comparing microhabitat availability to *Lachnolaimus maximus* on home ranges vs utilization during behavioral observations. Abundance is average percent cover of or occurrence over discriminating microhabitats (* = values presented are square root transformed as in SIMPER analysis), their contribution (%) to the observed dissimilarity, and the cumulative total (%) of contributions. Turf/macroalgae and live coral are not listed because of their low contributions to the observed dissimilarity. D = Jacob's electivity index, ranging from -1.0 to +1.0; negative values indicating avoidance, zero indicating random selection from the environment, and positive values indicating active selection or preference.

Microhabitat	Abundance*		Contribution	Cumulative	D
	Availability	Utilization			
Macroalgae	4.86	1.85	17.13	17.13	-0.704
Sandy rubble	1.48	3.06	13.11	30.24	0.579
Sandy turf	3.14	1.78	12.80	43.04	-0.385
Algal turf	2.41	2.90	11.92	54.96	0.001
Rubble	1.58	2.64	11.34	66.30	0.444
Sand	2.26	2.86	10.78	77.08	0.247
Gorgonian	2.13	2.82	9.35	86.42	0.305

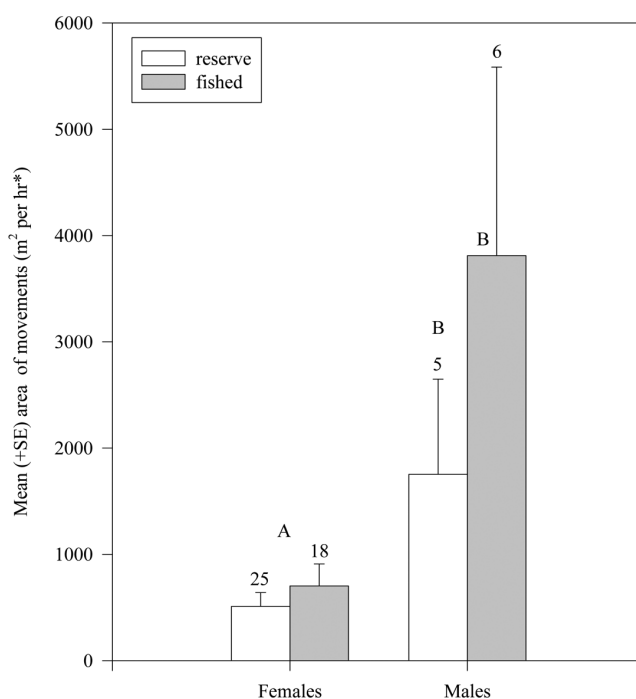


Figure 4. Mean (+SE) area of movements of *Lachnolaimus maximus* tracked in the Western Sambos reserve and Middle Sambos fished site. *Hogfish were observed for similar periods of time at both study sites (Mann-Whitney Rank Sum test, $t = 715$, $N_{\text{reserve}} = 30$, $N_{\text{fished}} = 24$, $P = 0.343$) and most observation periods lasted at least an hour. Numbers above bars indicate sample sizes and different letters indicate significant differences with the SNK test ($P < 0.05$).

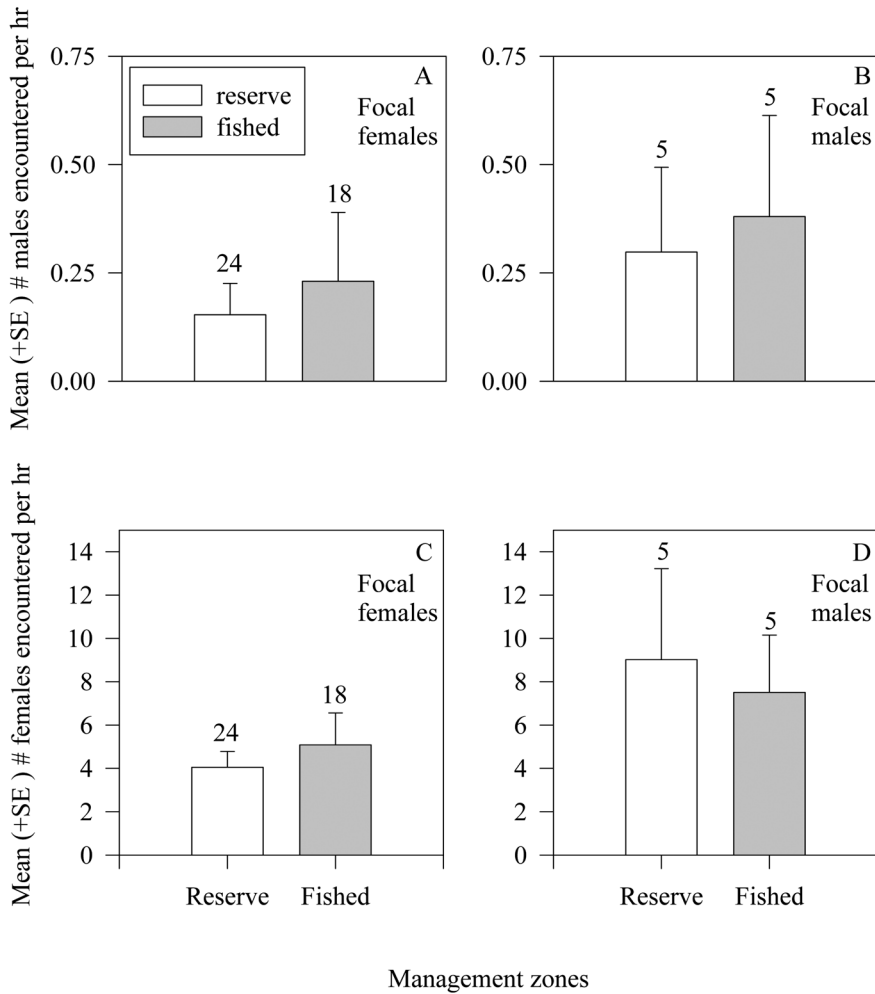


Figure 5. Mean (+SE) conspecific encounter rates recorded when following focal *Lachnolaimus maximus* in the Western Sambos reserve and Middle Sambos fished site. (A) Encounters with males recorded when following focal females. (B) Encounters with males recorded when following focal males. (C) Encounters with females recorded when following focal females. (D) Encounters with females recorded when following focal males. Numbers above bars indicate sample sizes. Note change in axis scale between upper and lower panels.

Encounters with males (Fig. 6A) and females (Fig. 6B) per unit of area for focal females tended to be greater in the reserve vs the fished site, suggesting that the relative abundance of both male and female hogfish might also be greater in the reserve compared to the fished site. In addition, although other females were encountered in 100% of focal female observations in both sites, encounters of males by focal females examined per ha occurred at nearly double the frequency in the reserve vs the fished site (Fig. 6A), despite the somewhat greater area surveyed at the fished site (Fig. 6C).

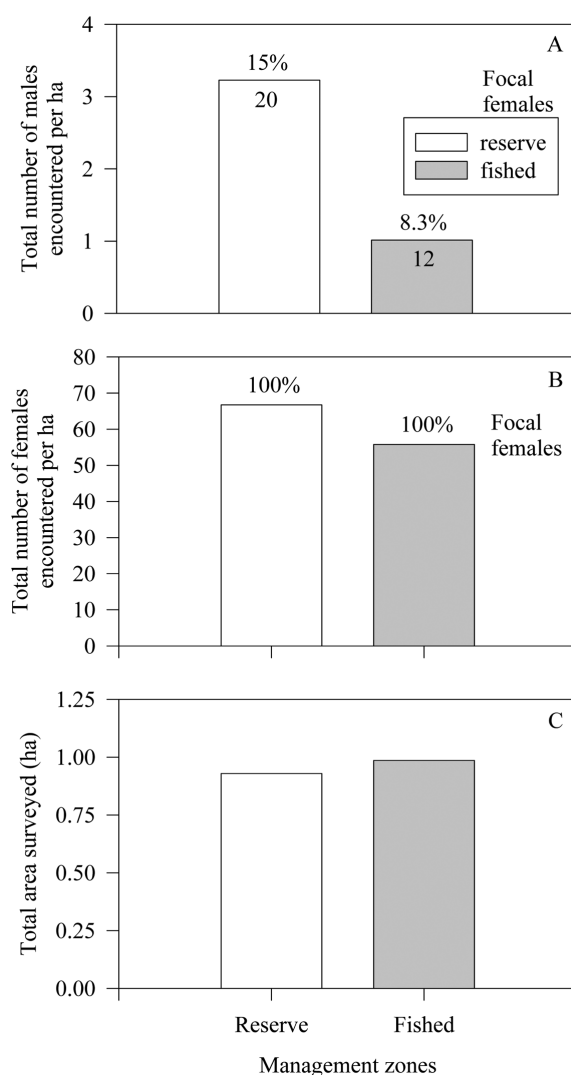


Figure 6. Encounters per hectare with males (A) and females (B) recorded when following focal female *Lachnolaimus maximus* in the Western Sambos reserve and Middle Sambos fished site. (C) Area surveyed during focal female observations. Numbers above bars in panels (A) and (B) indicate the proportion of observations where either males or females were encountered by focal females. Numbers within bars in panel (A) indicate sample sizes, which are the same for panels (B) and (C). Note change in axis scales.

DISCUSSION

Our observations of hogfish reproductive behavior in the Florida Keys National Marine Sanctuary, including the clustered arrangement and conspicuous patrolling of harem territories, with spawning events widely distributed throughout territories, closely resemble those studied previously for other harem-forming fishes, including wrasses, hawkfishes, pufferfishes, and parrotfishes (Thresher, 1984; Colin and

Bell, 1991; Muñoz and Warner, 2003; Adreani et al., 2004). The conspicuous and stereotypical reproductive behaviors that we observed in the FKNMS match those described previously off North Carolina (Parker, 2000) and in Puerto Rico (Colin, 1982), but these earlier studies did not observe focal individuals continuously during the spawning period and therefore reported no information on harem-specific reproductive output. We found vast differences in reproductive output between the Western Sambos Ecological Reserve and the Middle Sambos fished site. Our observations confirmed daily spawning for males controlling specific harem territories and McBride and Johnson (2007) suggest that females appear to spawn on a daily basis as well, based on gonad morphology. Extending our estimate of daily reproductive output through a peak 5 mo spawning season suggests a representative harem in the reserve contributes approximately 4.8 million eggs per season. Given the spatial distribution of harem territories in the reserve, annual estimates may translate into tens of millions of larval propagules output from the reserve relative to severely reduced output from the fished site. Why was reproduction virtually absent at the fished site? Although we observed one incidence of courtship at the fished site, this important observation was made after having already devoted a 3–4 times greater survey effort there and further serves to underscore the dramatic differences in reproduction between sites. We do not argue that no reproduction takes place at the fished site, only that reproductive output is severely reduced in comparison to the reserve.

Our analyses of microhabitats present on home ranges and microhabitat utilization patterns indicate similarities in these parameters between study sites. We found that hogfish actively selected sandy rubble, rubble, sand, and gorgonian microhabitats, in agreement with previous qualitative reports that hogfish can be found along reef edges in areas of abundant gorgonians and open sand (Randall and Warmke, 1967; Davis, 1976; McBride and Johnson, 2007). Hogfish feed primarily on sand-dwelling mollusks (Randall and Warmke, 1967) but have also been implicated in the top-down control of sea urchins (McClanahan, 1999), and may be a potentially important structuring force in the ecology of coral reefs (Knowlton, 1992; Hughes, 1994). Using focal observations of 667 feeding events by hogfish in the Florida Keys, Clifton and Motta (1998) demonstrated that nearly all feeding occurred in sand or coral rubble substrata. Together, these data suggest that essential fish habitat for adult hogfish includes gorgonian areas and rubble habitats with sand.

Our observations of individual hogfish movements and encounter rates with conspecifics indicate that males moved more than females regardless of site and that encounter rates between hogfish did not differ between sites. Although non-significant, the underlying trends that we observed for hogfish encounters and movements could be interpreted as preliminary evidence that key social processes may differ between sites, with apparent dramatic consequences to reproductive output. Whereas female hogfish tended to encounter male and female conspecifics more often at the fished site compared with the reserve, focal male hogfish tended to encounter females more often in the reserve than at the fished site. Together with the observation that males at the fished site may rove more extensively than males in the reserve, this suggests that encounters of focal females with males in the fished site may involve a variety of different individual males. In addition, hogfish appear more abundant in the reserve than in the fished site, as suggested by female encounters with conspecifics per unit area. In the Turks and Caicos, hogfish occurred at larger sizes and higher densities in a reserve compared to fished sites (Tupper and Rudd, 2002) and similar (though non-

significant) trends are apparent at other sites in the Florida Keys (Keller et al., 2003; Ault et al., 2006). Assuming this variation in hogfish abundance with management regime, one might expect, in the absence of social factors, higher encounter rates with males and females in the reserve. Instead, the patterns in our behavioral data imply an alternative scenario and suggest that social factors are operating differently in the reserve and fished sites.

A SOCIAL BREAKDOWN HYPOTHESIS FOR LACK OF REPRODUCTION AT THE MIDDLE SAMBOS FISHED SITE.—Intraspecific interactions (both inter- and intrasexual) can be stabilizing to animal social systems, for example, in the establishment and maintenance of territories (Gladstone, 1994; Donaldson, 1995; Zabala et al., 1997) or in the evaluation of whether or not to change sex (Munday et al., 2006). For many sex changing organisms, cues for sex change appear to be sensitive to the immediate social environment and may be based on relative size, sex ratio, or local population density (Munday et al., 2006). At the fished site, regular harvesting should continue to remove the largest individuals, which typically are males, as has been shown for hogfish in Florida (McBride and Richardson, 2007). At heavily fished sites, therefore, we hypothesize that the frequency of intraspecific interactions and change in the identity of the participants suggested by the underlying (non-significant) trends in our encounter rate data may leave females and remaining males constantly reassessing their places in the social hierarchy or reestablishing their territory boundaries, leading to the destabilization of social structure and sharply decreasing reproduction relative to sites protected within reserves. There are examples of previously studied protogynous species that are consistent with this hypothesis. Repeated removals in the field of male Japanese angelfish, *Centropyge interruptus* (Tanaka, 1918), show that multiple individuals from different harems can be affected and respond to altered social conditions (Moyer and Nakazono, 1978), while some harem halfmoon triggerfish, *Sufflamen chrysopteron* (Bloch and Schneider, 1801), that began sex change following male removals had not acquired mates and were not observed to spawn 90–94 d following removals (Takamoto et al., 2003).

In contrast, our behavioral observations suggest that interactions that have a stabilizing effect appear to occur more frequently in the reserve. There, regular patrols by individual males should allow territory boundaries to be established and once established, these boundaries would result in decreased male-male encounters through the “dear enemy effect” (Fisher, 1954). This hypothesis proposes that territorial individuals recognize their neighbors and should show respect for neighboring territory boundaries (review in Ydenberg et al., 1988). Additionally, regular visits by males with females should stabilize the mating system by allowing females to more accurately assess their social status and by making the benefits of investment in reproduction or sex change clear. The underlying trend of encounters that we recorded at both study sites is consistent with these hypotheses, suggesting stable, established social groups in the reserve and the opposite in the fished site, while the tracks recorded from spawning fish reveal the persistence of reproductive harems and predictable social system that are possible in protected locations.

We caution, however, that the power from statistical comparisons of encounter rates reflects the fact that these trends are based on only limited observations. We would have liked to incorporate additional study sites to help understand the variance in behavior associated with reserve and fished sites, but time and inclement weather precluded this possibility. Additional observations are needed to confirm

the prevalence of this trend throughout the range of *L. maximus* and to allow robust generalities regarding reproductive and social behavior to become apparent (e.g., extent of female fidelity to a harem; degree of male territoriality outside the spawning period).

One may argue that perhaps we did not observe reproduction at the fished site because hogfish might exhibit differential responses to observers (negative [escape] at the fished site and positive in the reserve), which could affect our ability to track and observe hogfish spawning between sites. Exploited species are known to exhibit differential responses to divers in areas of differing disturbance (fished vs reserve; Cole, 1994; Kulbicki, 1998) but three factors suggest that these responses did not bias our results. First, we conducted all behavioral observations on snorkel rather than with scuba, often times located 3–4 m above a focal animal. Second, while many behavioral studies employ short (1–15 min) acclimation and observation periods, we tracked fish for hour-long periods and continuously during the spawning period (1400–1800), which afforded focal animals extensive periods of time to acclimate to our presence. Third, within the context of diver effects on fish behavior, *L. maximus* is a good example of a neutral or even curious species (i.e., one that investigates or does not flee an observer that intrudes into its range, Kulbicki, 1998), making it an ideal choice for a study such as ours. At the same time, however, this natural behavioral response of hogfish to observers increases their susceptibility to capture by spearfishing.

KEY CHARACTERISTICS THAT HAVE THE POTENTIAL TO MAKE HOGFISH VULNERABLE TO EXPLOITATION.—Hogfish are highly valued by both commercial and recreational divers, are a favorite target of spearfishers, and are one of the most economically valuable wrasses in the western North Atlantic ocean (Davis, 1976; McBride and Murphy, 2003; McBride and Johnson, 2007). *Lachnolaimus maximus* show high fidelity to reproductive territories that they conspicuously and regularly patrol, and this adds to the ease with which they can be targeted by spearfishers (Alonzo et al., 2004; Hamilton et al., 2007). Numerous internet sites are devoted entirely to their capture and contain discussions of the very behaviors previously mentioned, touting their suitability for beginning spearfishers related to the supposed “dumb” nature of hogfish (e.g., HogFishWorld.com, 2002; Kat, 2007).

Not only are hogfish highly prized and easily speared, but particular elements of their protogynous life history and complex social system may increase their vulnerability to overexploitation. For hogfish, the actual process of sex change appears relatively slow, as McBride and Johnson (2007) found transitional (in the process of changing sex) individuals to be most common from July through September, following the spawning season. They suggested that *L. maximus* might initiate sex change following the spawning season, as in gag grouper, *Mycteroperca microlepis* (Goode and Bean, 1879) (McBride and Johnson, 2007). In *M. microlepis* or red hind, *Epinephelus guttatus* (Linnaeus, 1758), males and females normally occur at low density in distinct habitats and social cues that influence the decision of whether or not to change sex are likely assessed at the spawning site; following assessment, sex-changed individuals return the following season as the changed sex (Shapiro et al., 1994; Coleman et al., 1996). Although *L. maximus* may undergo a protracted period of sex change following the spawning season, this species can likely assess social cues throughout the year as males and females occur in similar habitats and regularly interact (R. Muñoz, pers. obs.).

Many species with social and mating systems in which large males monopolize mating opportunities are protogynous hermaphrodites and show sex ratios that are naturally skewed towards females (Leonard, 2006; Munday et al., 2006). Because fishing typically removes the largest individuals, fishing these species tends to differentially remove males who are already in short supply, and this can lead to sperm limitation in populations where not all eggs are fertilized (Warner et al., 1995). Where sex change is under social control and where females can respond to fishing-induced changes in the local environment, the problem of sperm limitation might be offset by female sex change; however, the reproductive output of the population would still decline as female egg production is lost to sex change. For *L. maximus*, the extent of disruption to reproductive activity could be worse than a simple decrease in output because we do not know if social control can produce sex-changed males from within the local social group when they are removed by fishing, if bachelor males take over reproductive groups when a vacancy arises, or if spawning territories dissolve and females disperse to other reproductive groups upon the disappearance of a male (Roberts and Polunin, 1991; McBride and Murphy, 2003; McBride and Johnson, 2007). Once abandoned, reproductive territories may never be reoccupied or may reform in areas more accessible to fishing if their method of establishment depends on social learning or tradition, as has been found in both reef and non-reef fish (Warner, 1988, 1990; Rose, 1993; Sadovy and Domeier, 2005). For example, experimental evidence with the bluehead wrasse, *Thalassoma bifasciatum* (Bloch, 1791) indicates previously used spawning sites were no more likely to be chosen by a newly introduced population when the original population was removed (Warner, 1988, 1990).

MANAGEMENT IMPLICATIONS AND THE ROLE OF NO-TAKE MARINE RESERVES.—A sex-changing life history, high site fidelity, and complex social structure are features shared by many economically important reef fishes and are associated with fishes that are vulnerable to overexploitation. These behavioral and life history characteristics may render ineffective traditional regulations such as minimum size limits and thus appear to have contributed to the failure of conventional management measures to stem the effects of fishing pressure on numerous reef fishes (Coleman et al., 2000). Despite minimum-size regulations (305 mm fork length, FL) on hogfish landings in Florida, *L. maximus* is on the International Union for Conservation of Nature (IUCN) Red List of vulnerable species and was recently listed as a Species of Greatest Conservation Need in Florida (Florida Fish and Wildlife Conservation Commission, 2005). Although McBride and Murphy (2003) indicated that maximum yield-per-recruit for hogfish would occur at a size larger than the current mean size of fish harvested (Florida Fish and Wildlife Conservation Commission, 2006), increased minimum size limits may still be problematic because they would continue to allow the removal of the largest, most reproductively successful individuals from the population. McBride and Johnson (2007) suggested that first-year male *L. maximus* may have lower reproductive success than older, more mature males, an idea consistent with our preliminary evidence of a positive (though non-significant) relationship between the number of matings vs male size. Two confamilials whose social and mating systems closely resemble that of *L. maximus*, the Mexican hogfish, *Bodianus diplotaenia* (Gill, 1862) and the California sheephead, *Semicossyphus pulcher* (Ayres, 1854), are also characterized by differential male reproductive success related to size (Hoffman et al., 1985; Adreani et al., 2004).

For protogynous fishes with complex social and mating systems, effective management may require alternative regulations and more thorough investigations into the social systems and sexual patterns of these species (Coleman et al., 2000; Hamilton et al., 2007; Pears et al., 2007). For these kinds of fishes, no-take marine reserves represent a management strategy that should allow the persistence of high levels of reproductive output by maintaining intact the social systems of larger (and more fecund) animals reproducing in reserves (Alonzo and Mangel, 2004). The use of discrete spawning territories by numerous reef fishes and the size of these territories for *L. maximus* emphasize the ability of even relatively small reserves, if carefully placed, to protect essential fish habitat such as spawning sites. Detailed ecological investigations conducted in situ provide a reliable means of identifying and confirming these critical locations and their associated habitat features.

For *L. maximus* and other similar reef fishes outside the protection of no-take reserves, slot limits (minimum and maximum size limits) would allow continued reproductive output by the largest females with the greatest fecundities and would also prevent the removal of the largest males, inhibiting the dissolution of the most productive harem territories. If additional studies confirm the prevalence of the patterns reported here, a blanket ban on the harvest of males during the spawning season should avoid the social breakdown of reproductive groups and might be warranted. Variations of such regulations are already well established and accepted by the general public with crustacea, for example, where females with eggs are not harvested. Mature male hogfish are easily differentiated from females due to external coloration (Colin, 1982; McBride and Johnson, 2007) and simple public education could occur with fliers posted in dive and tackle shops.

Our study in the Western Sambos Ecological Reserve and the Middle Sambos fished site underscores that field-based studies employing direct, in situ sampling methods such as snorkeling and diving will remain as valuable tools to scientists and managers because they can reveal mechanisms of impact to fishery resources that indirect sampling such as fishing, trapping, or remote sensing cannot. For site-attached fishes with complex social and mating systems, no-take reserves may play a key role in the maintenance of reproductive output beyond simple increases in biomass by allowing for the persistence and stability of social structure and by protecting essential fish habitat such as spawning sites. Fished areas outside reserves, in contrast, may generate less reproductive output for these species than we once thought.

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LITERATURE CITED

- Abesamis, R. A. and G. R. Russ. 2005. Density-dependent spillover from a marine reserve: long-term evidence. *Ecol. Appl.* 15: 1798–1812.
- Adreani, M. S., B. E. Erisman, and R. R. Warner. 2004. Courtship and spawning behavior in the California sheephead, *Semicossyphus pulcher* (Pisces: Labridae). *Environ. Biol. Fish.* 71: 13–19.
- Afonso, P., J. Fontes, K. N. Holland, and R. S. Santos. 2008. Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. *Mar. Ecol. Prog. Ser.* 359: 215–227.
- Alonzo, S. H. and M. Mangel. 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fish. Bull.* 102: 1–13.
- _____, M. Key, T. Ish, and A. D. MacCall. 2004. Status of the California sheephead (*Semicossyphus pulcher*) stock (2004). California Department of Fish and Game, Monterey, CA. 146 p. Available from: <http://www.dfg.ca.gov/marine/sheephead2004/pdfs/entire.pdf> Accessed 2 March 2009.
- Ault, J. S., S. G. Smith, J. A. Bohnsack, J. G. Luo, D. E. Harper, and D. B. McClellan. 2006. Building sustainable fisheries in Florida's coral reef ecosystem: positive signs in the Dry Tortugas. *Bull. Mar. Sci.* 78: 633–654.
- Bartholomew, A., J. A. Bohnsack, S. G. Smith, J. S. Ault, D. E. Harper, and D. B. McClellan. 2008. Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. *Landsc. Ecol.* 23: 55–65.
- Beets, J. and A. Friedlander. 1999. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environ. Biol. Fish.* 55: 91–98.
- Bohnsack, J. A., D. B. McClellan, D. E. Harper, G. S. Davenport, G. J. Konoval, A. Eklund, J. P. Contillo, S. K. Bolden, P. C. Fischel, G. S. Sandorf, et al. 1999. Baseline data for evaluating reef fish populations in the Florida Keys, 1979–1998. NOAA Technical Memorandum NMFS-SEFSC-427. Miami, FL. 61 p. Available from: <http://www.sefsc.noaa.gov/PDFdocs/427techmemo.pdf> Accessed 2 March 2009.
- Branch, G. M. and F. Odendaal. 2003. The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. *Biol. Conserv.* 114: 255–269.
- Burton, M. L., K. J. Brennan, R. C. Muñoz, and R. O. Parker. 2005. Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's Hump two years after establishment of the Tortugas South Ecological Reserve. *Fish. Bull.* 103: 404–410.
- Chapman, M. R. and D. L. Kramer. 2000. Movements of fishes within and among fringing coral reefs in barbados. *Environ. Biol. Fish.* 57: 11–24.
- Chateau, O. and L. Wantiez. 2007. Site fidelity and activity patterns of a humphead wrasse, *Cheilinus undulatus* (Labridae), as determined by acoustic telemetry. *Environ. Biol. Fish.* 80: 503–508.
- Choat, J. H. 1991. The biology of herbivorous fishes on coral reefs. Pages 120–155 in P. F. Sale, ed. *The ecology of fishes on coral reefs*. Academic Press, San Diego.
- Clifton, K. B. and P. J. Motta. 1998. Feeding morphology, diet, and ecomorphological relationships among five Caribbean labrids (Teleostei, Labridae). *Copeia* 1998: 953–966.
- Cole, R. G. 1994. Abundance, size structure, and diver-oriented behavior of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. *Biol. Conserv.* 70: 93–99.
- Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environ. Biol. Fish.* 47: 129–141.

- Coleman, F. C., C. C. Koenig, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, R. W. Chapman, G. R. Sedberry, and C. B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries* 25: 14–21.
- Colin, P. L. 1982. Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae). *Fish. Bull.* 80: 853–862.
- _____, and L. J. Bell. 1991. Aspects of the spawning of labrid and scarid fishes (Pisces, Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. *Environ. Biol. Fish.* 31: 229–260.
- Cox, C. and J. H. Hunt. 2005. Change in size and abundance of Caribbean spiny lobsters *Panulirus argus* in a marine reserve in the Florida Keys National Marine Sanctuary, USA. *Mar. Ecol. Prog. Ser.* 294: 227–239.
- Davis, J. C. 1976. Biology of the hogfish, *Lachnolaimus maximus* (Walbaum), in the Florida Keys. M. S. Thesis, University of Miami, Coral Gables. 87 p.
- DeMartini, E. E. 1993. Modeling the potential of fishery reserves for managing Pacific coral-reef fishes. *Fish. Bull.* 91: 414–427.
- Donaldson, T. J. 1995. Partitioning behavior and intraspecific and interspecific interactions—a comparison between male and female groupers, *Cephalopholis spiloparaea* (Pisces, Serranidae, Epinephelinae). *Mar. Biol.* 121: 581–584.
- Eristhee, N. and H. A. Oxenford. 2001. Home range size and use of space by Bermuda chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufriere Marine Management Area, St Lucia, West Indies. *J. Fish Biol.* 59: 129–151.
- Evans, R. D., G. R. Russ, and J. P. Kritzer. 2008. Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves on the Great Barrier Reef, Australia. *Coral Reefs* 27: 179–189.
- Fisher, J. 1954. Evolution and bird sociality. Pages 71–83 in J. Huxley, A. C. Hardy, and E. B. Ford, eds. *Evolution as a process*. Allen and Unwin, London.
- Florida Fish and Wildlife Conservation Commission. 2000. Benthic habitats of the Florida Keys. FMRI Technical Report TR-4. Fish and Wildlife Research Institute, St. Petersburg, FL. 59 p. Available from: http://www.floridamarine.org/engine/download_redirection_process.asp?file=benthic%5Fatlas%5F4544%2Epdf&objid=23848&dltpe=publication Accessed 2 March 2009.
- _____. 2005. Florida's Wildlife Legacy Initiative. Florida's Comprehensive Wildlife Conservation Strategy. Tallahassee, FL. 530 p. Available from: http://www.myfwc.com/docs/WildlifeHabitats/Legacy_Strategy.pdf Accessed 2 March 2009.
- _____. 2006. Hogfish (*Lachnolaimus maximus*). Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute 5233. St. Petersburg, FL. 5 p. Available from: http://www.floridamarine.org/engine/download_redirection_process.asp?file=Hogfish.pdf&objid=5233&dltpe=article Accessed 2 March 2009.
- Gell, F. R. and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18: 448–455.
- Gladstone, W. 1994. Lek-like spawning, parental care and mating periodicity of the triggerfish *Pseudobalistes flavimarginatus* (Balistidae). *Environ. Biol. Fish.* 39: 249–257.
- Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13: S117–S137.
- Hamilton, S. L., J. E. Caselle, J. D. Standish, D. M. Schroeder, M. S. Love, J. A. Rosales-Casian, and O. Sosa-Nishizaki. 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecol. Appl.* 17: 2268–2280.
- Helfman, G. S., J. L. Meyer, and W. N. McFarland. 1982. The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). *Anim. Behav.* 30: 317–326.
- Hoffman, S. G., M. P. Schildhauer, and R. R. Warner. 1985. The costs of changing sex and the ontogeny of males under contest competition for mates. *Evolution* 39: 915–927.

- HogFishWorld.com; Hog Knowledge [Internet]. Bahamas; 26 January 2003, © 2002. Available from: <http://www.hogfishworld.com/hogknowledge.html> Accessed 31 August 2008.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551.
- Jaap, W. C. 1979. Observations on zooxanthellae expulsion at Middle Sambo reef, Florida Keys. *Bull. Mar. Sci.* 29: 414–422.
- Jacobs, J. 1974. Quantitative measurement of food selection. *Oecologia* 14: 413–417.
- Jennings, S., E. M. Grandcourt, and N. V. C. Polunin. 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* 14: 225–235.
- Kat. Spearfishing for hogfish in Key West. Flight to Key West. 1 October 2007. Available from: <http://flight-to-key-west.blogspot.com/2007/10/spearfishing-for-hogfish-in-key-west.html> Accessed 31 August 2008.
- Keller, B. D. and S. Donahue. 2006. 2002-03 sanctuary science report: an ecosystem report card after five years of marine zoning. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Office of National Marine Sanctuaries, Florida Keys National Marine Sanctuary, Marathon, FL. 378 p. Available from: http://floridakeys.noaa.gov/research_monitoring/final_draft.pdf Accessed 2 March 2009.
- _____, J. Delaney, and B. Causey. 2003. Monitoring changes in the fully protected zones of the Florida Keys National Marine Sanctuary. *Proc. Gulf Caribb. Fish. Inst.* 54: 694–701.
- Kerwath, S. E., A. Gotz, C. G. Attwood, W. H. H. Sauer, and C. G. Wilke. 2007. Area utilisation and activity patterns of roman *Chrysoblephus laticeps* (Sparidae) in a small marine protected area. *Afr. J. Mar. Sci.* 29: 259–270.
- Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.* 32: 674–682.
- Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bull. Mar. Sci.* 66: 593–616.
- Kramer, D. L. and M. R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. *Environ. Biol. Fish.* 55: 65–79.
- Kulbicki, M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *J. Exp. Mar. Biol. Ecol.* 222: 11–30.
- Leonard, J. L. 2006. Sexual selection: lessons from hermaphrodite mating systems. *Integr. Comp. Biol.* 46: 349–367.
- Lowe, C. G., D. T. Topping, D. P. Cartamil, and Y. P. Papastamatiou. 2003. Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take marine reserve. *Mar. Ecol. Prog. Ser.* 256: 205–216.
- Martin, P. and P. Bateson. 1993. Measuring behavior: an introductory guide. Cambridge University Press, Cambridge. 222 p.
- McBride, R. S. and M. D. Murphy. 2003. Current and potential yield per recruit of hogfish, *Lachnolaimus maximus*, in Florida. *Proc. Gulf Caribb. Fish. Inst.* 54: 513–525.
- _____, and M. R. Johnson. 2007. Sexual development and reproductive seasonality of hogfish (Labridae: *Lachnolaimus maximus*), an hermaphroditic reef fish. *J. Fish Biol.* 71: 1270–1292.
- _____, and A. K. Richardson. 2007. Evidence of size-selective fishing mortality from an age and growth study of hogfish (Labridae: *Lachnolaimus maximus*), a hermaphroditic reef fish. *Bull. Mar. Sci.* 80: 401–417.
- _____, P. E. Thurman, and L. H. Bullock. 2008. Regional variations of hogfish (*Lachnolaimus maximus*) life history: consequences for spawning biomass and egg production models. *J. Northwest Atl. Fish. Sci.* 41: 1–12.
- McClanahan, T. R. 1999. Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. *Ecosystems* 2: 511–523.

- McGovern, J. C., G. R. Sedberry, H. S. Meister, T. M. Westendorff, D. M. Wyanski, and P. J. Harris. 2005. A tag and recapture study of gag, *Mycteroperca microlepis*, off the southeastern US. *Bull. Mar. Sci.* 76: 47–59.
- Meyer, C. G. and K. N. Holland. 2005. Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environ. Biol. Fish.* 73: 201–210.
- Miller, M. W. and C. L. Gerstner. 2002. Reefs of an uninhabited Caribbean island: fishes, benthic habitat, and opportunities to discern reef fishery impact. *Biol. Conserv.* 106: 37–44.
- Molloy, P. P., J. D. Reynolds, M. J. G. Gage, L. Mosqueirac, and I. M. Cote. 2008. Links between sex change and fish densities in marine protected areas. *Biol. Conserv.* 141: 187–197.
- Moyer, J. T. and A. Nakazono. 1978. Population structure, reproductive behavior and protogynous hermaphroditism in the angelfish *Centropyge interruptus* at Miyake-jima, Japan. *Jpn. J. Ichthyol.* 25: 25–39.
- Munday, P. L., P. M. Buston, and R. R. Warner. 2006. Diversity and flexibility of sex-change strategies in animals. *Trends Ecol. Evol.* 21: 89–95.
- Muñoz, R. C. and P. J. Motta. 2000. Interspecific aggression between two parrotfishes (*Sparisoma*, Scaridae) in the Florida Keys. *Copeia* 2000: 674–683.
- _____. and R. R. Warner. 2003. Alternative contexts of sex change with social control in the bucktooth parrotfish, *Sparisoma radians*. *Environ. Biol. Fish.* 68: 307–319.
- Nanami, A. and H. Yamada. 2008. Size and spatial arrangement of home range of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef determined using a portable GPS receiver. *Mar. Biol.* 153: 1103–1111.
- Nemeth, R. S., J. Blondeau, S. Herzlieb, and E. Kadison. 2007. Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environ. Biol. Fish.* 78: 365–381.
- Nursall, J. R. 1977. Territoriality in redlip blennies (*Ophioblennius atlanticus*-Pisces: Blenniidae). *J. Zool. (Lond.)* 182: 205–223.
- Parker, R. O. 2000. Courtship in hogfish, *Lachnolaimus maximus*, and other behavior of reef fishes off Beaufort, North Carolina. *J. Elisha Mitchell Sci. Soc.* 116: 260–261.
- Pears, R. J., J. H. Choat, B. D. Mapstone, and G. A. Begg. 2007. Reproductive biology of a large, aggregation-spawning serranid, *Epinephelus fuscoguttatus* (Forsskal): management implications. *J. Fish Biol.* 71: 795–817.
- Petersen, C. W. and R. R. Warner. 2002. The ecological context of reproductive behavior. Pages 103–118 in P. F. Sale, ed. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego.
- Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Technical Memorandum NMFS-SEFC-261. Miami, FL. 40 p. Available from: <http://www.safmc.net/Portals/6/Library/MPAs%20Source%20Documents/NOAA%20Technical%20MemoNMFSSEFC261.pdf> Accessed 2 March 2009.
- Randall, J. E. and G. L. Warmke. 1967. The food habits of the hogfish (*Lachnolaimus maximus*), a labrid fish from the Western Atlantic. *Caribb. J. Sci.* 7: 141–144.
- Reeson, P. H. 1983. The biology, ecology and bionomics of the parrotfishes, Scaridae. Pages 166–177 in J. L. Munro, ed. *Caribbean coral reef fishery resources*. International Center for Living Aquatic Resources Management, Manila.
- Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153: 1–6.
- Roberts, C. M. 2000. Selecting marine reserve locations: optimality versus opportunism. *Bull. Mar. Sci.* 66: 581–592.
- _____. and N. V. C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.* 1: 65–91.
- Rodwell, L. D., E. B. Barbier, C. M. Roberts, and T. R. McClanahan. 2003. The importance of habitat quality for marine reserve fishery linkages. *Can. J. Fish. Aquat. Sci.* 60: 171–181.

- Rose, G. A. 1993. Cod spawning on a migration highway in the north-west Atlantic. *Nature* 366: 458–461.
- Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. Pages 421–443 in P. F. Sale, ed. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego.
- _____, and A. C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral-reef fishes. *Mar. Ecol. Prog. Ser.* 56: 13–27.
- Sadovy, Y. and M. Domeier. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs* 24: 254–262.
- Sale, P. F. 1991. Introduction. Pages 3–15 in P. F. Sale, ed. *The ecology of fishes on coral reefs*. Academic Press, San Diego.
- _____, R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, et al. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends Ecol. Evol.* 20: 74–80.
- Shapiro, D. Y., G. Garcia-Moliner, and Y. Sadovy. 1994. Social system of an inshore stock of the red hind grouper, *Epinephelus guttatus* (Pisces, Serranidae). *Environ. Biol. Fish.* 41: 415–422.
- Takamoto, G., S. Seki, Y. Nakashima, K. Karino, and T. Kuwamura. 2003. Protogynous sex change in the harem triggerfish *Sufflamen chrysopterus* (Tetraodontiformes). *Ichthyol. Res.* 50: 281–283.
- Tetreault, I. and R. F. Ambrose. 2007. Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. *Ecol. Appl.* 17: 2251–2267.
- Thompson, R. and J. L. Munro. 1983. The biology, ecology and bionomics of the hinds and groupers, Serranidae. Pages 59–81 in J. L. Munro, ed. *Caribbean coral reef fishery resources*. International Center for Living Aquatic Resources Management, Manila.
- Thresher, R. E. 1984. Reproduction in reef fishes. TFH Publications, Neptune City. 399 p.
- Tupper, M. H. 2007. Spillover of commercially valuable reef fishes from marine protected areas in Guam, Micronesia. *Fish. Bull.* 105: 527–537.
- _____, and M. A. Rudd. 2002. Species-specific impacts of a small marine reserve on reef fish production and fishing productivity in the Turks and Caicos Islands. *Environ. Conserv.* 29: 484–492.
- U.S. Department of Commerce. 1996. Florida Keys National Marine Sanctuary final management plan/environmental impact statement, Vol. 1. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Silver Spring, MD. 319 p. Available from: <http://floridakeys.noaa.gov/regs/fmp1.pdf> Accessed 2 March 2009.
- Warner, R. R. 1988. Traditionality of mating-site preferences in a coral reef fish. *Nature* 335: 719–721.
- _____. 1990. Resource assessment versus tradition in mating-site determination. *Am. Nat.* 135: 205–217.
- _____, and D. R. Robertson. 1978. Sexual patterns in the labroid fishes of the Western Caribbean, I: the wrasses (Labridae). *Smithson. Contrib. Zool.* 254: 1–27.
- _____, D. Y. Shapiro, A. Marconato, and C. W. Petersen. 1995. Sexual conflict-males with highest mating success convey the lowest fertilization benefits to females. *Proc. R. Soc. Lond. B Biol. Sci.* 262: 135–139.
- Warwick, R. M. 1993. Environmental-impact studies on marine communities-pragmatical considerations. *Aust. J. Ecol.* 18: 63–80.
- _____, and K. R. Clarke. 2001. Practical measures of marine biodiversity based on relatedness of species. *Oceanogr. Mar. Biol. Annu. Rev.* 39: 207–231.
- Williamson, D. H., G. R. Russ, and A. M. Ayling. 2004. No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ. Conserv.* 31: 149–159.

- Willis, T. J., R. B. Millar, R. C. Babcock, and N. Tolimieri. 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environ. Conserv.* 30: 97–103.
- Ydenberg, R. C., L. A. Giraldeau, and J. B. Falls. 1988. Neighbours, strangers, and the asymmetric war of attrition. *Anim. Behav.* 36: 343–347.
- Zabala, M., P. Louisy, A. GarciaRubies, and V. Garcia. 1997. Socio-behavioural context of reproduction in the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). *Sci. Mar.* 61: 79–98.

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